The Deep History of Life

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Nearly four billion years after they first evolved, microorganisms remain fundamental cogs in the highly interactive Earth system.

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The view down Lake Louise is easily one of North America's finest, with towering peaks framing crystalline blue waters. Standing along the lakeshore, I sense the same majesty as other hikers, but I also see something else—something equally grand, but in a different way. Our planet records its own history, written in sedimentary rocks deposited one layer on another through geologic time. In the mountains behind Lake Louise, then, I see a library, and if we know how to read its volumes, we can glimpse our world in formation.

I was first attracted to sedimentary rocks as a boy growing up in the foothills of the Appalachian Mountains. On weekends and summer days I loved nothing more than to split open limestones and shales, pulled from local hills and road cuts, to reveal fossil shells or leaves inside. I can't tell you which was more exciting, the sight of organisms that lived millions of years ago or the act of discovery, of unearthing fragments of life's history that no one had ever observed before. As I grew up, my twin loves of fossils and discovery persisted undiminished, although my quarry diminished quite a bit, at least in size. From childhood infatuation with dinosaurs, I graduated to a more realistic (in central Pennsylvania) search for brachiopods and corals, older if less scary than *T. rex*. Then, as a college student, I discovered a record of life still older—and much, much smaller.

The conventional fossil record is built of hard parts—bones, shells and decay-resistant organic tissues buried in the sediments that accumulate on floodplains, in lakes, and on the seafloor. As he wrote *The Origin of Species*, Charles Darwin was keenly aware of this record—and bothered by it. In particular, Darwin was unsettled by the oldest known fossils, trilobites preserved in mudstones near the base of the Cambrian System in Wales. Trilobites have bodies of impressive complexity—segmented bodies, jointed legs, and compound eyes—and so, Darwin reasoned, could not record Earth's earliest life. They must have been preceded by simpler forms that evolved complexity gradually over vast oceans of time. Where was the record of these earlier organisms? Darwin speculated that it lay buried beneath younger rocks, had been destroyed by erosion and metamorphism, or simply remained to be discovered in remote regions unvisited by Victorian geologists.

For nearly a century after publication of *The Origin of Species* (1859), the oldest fossils remained animal skeletons in Cambrian rocks. A few brave paleontologists reported microscopic fossils in older beds, but such claims were routinely dismissed by a skeptical community. Take, for example, a 1939 critique by Harvard paleontologist Percy Raymond: "Walcott leaves it to be accepted on faith that an organism without hard parts, and less than 0.001 millimeter in diameter, would be preserved in identifiable condition from pre-Cambrian time to the present!" Raymond's choice of punctuation tells us all we need to know about contemporary views on pre-Cambrian fossils.

In the 1950s, things began to change. First, geologists began the routine application of radioactive decay to problems of geologic age. The radioactive breakdown of unstable isotopes had been used to estimate the age of fossils as early as 1913, but only in the 1950s did laboratory innovations enter into productive partnership with geologic mapping. As a result, geologists came to understand that the oldest Cambrian fossils were about 542 million years old, but also that the Earth itself formed more than 4.6 billion years ago. Continuing research has pushed the age of the oldest known animals to about 650 million years, but what came earlier?

As geologists began to calibrate our planet's history, biologists discovered a molecular basis for building a tree of life that depicts the evolutionary relationships of all organisms, from elephants to *Escherichia coli*, redwoods to rotifers. Animals form only a small cluster of branches near the tip of one limb. By implication, then, the greater diversity of life, and life's deep evolutionary history, must be microbial.

The recognition that Earth's earliest inhabitants were microorganisms raises a particular challenge for paleontologists. Bacteria may be ancient and ubiquitous, but they are also tiny and seemingly fragile—could Earth's early microbial inhabitants have left a discernible signature in our planet's oldest sedimentary rocks? Remarkably (to most) and excitingly (to me), they could and did. In fact, the geologic record of microbial life is preserved in four distinct ways. First, bacteria and protists leave what we can consider an extension of the conventional fossil record: cell walls and extracellular envelopes preserved directly in sedimentary rocks. In 1953, my mentor, Elso Barghoorn, and his colleague Stanley Tyler first reported unambiguous microfossils of bacteria in Canadian rocks nearly 2 billion years old, nearly quadrupling the known history of life.

Second, microorganisms also leave molecular fossils that complement the record of morphology. Just as conventional fossils comprise decay-resistant remains like shells and bones, so, too, do some biological molecules have a good chance of avoiding decay. Unfortunately for paleontologists, proteins and nucleic acids rarely enter the geologic record—they are simply too good to eat. Lipids, however, are a different story. When you die, the last component of your body to disappear may well be the cholesterol laced through your cell membranes (and probably lining your arteries). Lipids made by bacteria, archaea, and unicellular eukaryotes occur abundantly in petroleum and other ancient organic deposits.

Sediments transported across the seafloor interact physically with microbial mat communities, providing a third and distinctly different biological signature in sedimentary rocks. Especially when the precipitation of mineral cements causes microbially influenced layers to accrete vertically into three-dimensional structures called stromatolites, the signature of ancient microorganisms can be massive. Microbial reefs in Precambrian sedimentary successions can be as large as those built today by corals and algae.

Finally, microbial populations can actually influence the composition of seawater, providing a distinct chemical signature in minerals precipitated from ancient oceans. For example, when photosynthetic organisms incorporate carbon dioxide into organic matter, they preferentially use CO_2 containing ^{12}C, the lighter stable isotope of carbon. Because of this, limestones and organic matter deposited on the seafloor preserve a record of primary production in the sea above them. In similar fashion, bacterial respiration using sulfate instead of oxygen preferentially uses SO_4^{2-} containing ^{32}S, the lightest isotopic form of sulfur, imparting a chemical record of the biologic sulfur cycle into gypsum and fool's gold formed in the oceans and underlying sediments.

The records of ancient microbial life, then, may be more subtle than dinosaur bones strewn across a valley floor, but they are no less abundant if you know how to look for them. For much of the past three decades, I've worked to discover and read these paleobiological records of Earth's oldest life, and to do so in a systematic way that reveals evolutionary pattern. I've spent long summers climbing cliffs in the Arctic, piloting rafts down Siberian rivers, and swatting flies in the outback of Australia—the quest to understand life's early history remains an act of exploration, in both time and space. But the record is there, and it makes sense in light of predictions from the tree of life. Sedimentary rocks just older than those that contain the earliest known animals preserve protozoa and simple algae, as well as cyanobacteria and other prokaryotes that must have been ubiquitous in shallow seas. Double the antiquity, to more than 1.5 billion years, and records of prokaryotes remain abundant, while those of eukaryotic microorganisms grow sparse. Double the age again, to more than 3 billion years, and the record becomes fragmentary and hard to interpret with confidence. One fact, however, stands out: the oldest sedimentary rocks available for study contain a clear signature of life. Earth has been a biological planet since its youth—and for most of our planet's long history, that life was microbial.

We can hazard only broad guesses about the biological properties of early microorganisms, but can make one key statement with confidence: early cells lived without oxygen. The evidence for this is iron-clad, both figuratively and literally. Distinctive rocks called banded iron formations (BIF) occur in many sedimentary deposits formed before 2.4 billion years ago. These rocks, major sources of the iron used industrially, cannot form in modern oceans for the simple reason that iron is effectively insoluble in oxygen-rich seawater and so cannot be transported by ocean currents. Ancient iron formations show that early oceans were different; they must have been oxygen-free throughout most of their depths, allowing iron to move in solution from place to place before precipitating out at sites of BIF deposition. Other geological observations corroborate this view, but about 2.4 billion years ago, the sedimentary record began to change. Rock chemistry tells us quite clearly that oxygen was beginning to accumulate in the atmosphere and surface oceans, and biology makes it clear that the source of that oxygen was cyanobacteria, the bacterial inventors of what biologists insist on calling "green plant" photosynthesis. The world that emerged, however, was not our own, but rather a long-lived intermediate biosphere in which moderately oxygen-rich surface oceans lay above subsurface waters that tended to be anoxic, and, indeed, rich in sulfide. How do we know this? Iron, again, provides our principal clues to Earth's middle age, as iron minerals in seafloor muds record the chemistry of overlying waters. When, then, did our oxygen-rich world take shape? Only, it seems, about 600-550 million years ago, just as animals with high rates of oxygen consumption began to appear in the fossil record.

In short, the story that has emerged, piece by piece, from field research in the Arctic, in Australia, in Siberia, and in a number of other places, is one with three grand chapters. In chapter one, the first 2 billion years of our planet's history, oxygen was sparse, but iron abundant—this is the world in which life emerged, and these were the environments that shaped the most fundamental features of biochemistry and ecology. Then, beginning about 2.4 billion years ago, the page turned to chapter two, Earth's long-lasting middle age, with moderate amounts of oxygen in the atmosphere and surface oceans, but, commonly, sulfidic waters beneath that oxic veneer. Eukaryotic cells evolved, expanding the ecological possibilities of microbial communities, but bacteria continued dominate the carbon cycle. Eukaryotic microorganisms began their rise to ecological prominence about 800 million years ago, as the sulfidic floor to the surface ocean began to dissipate, and with a second increase in oxygen levels 600-550 million years ago, our familiar world of animals and plants began to take shape.

Decades after leaving the Appalachians, I still get a thrill from fossils and continue to enjoy the detective work of reconstructing evolutionary history from the biological and chemical details of ancient rocks. Conventional fossils—the bones and shells that fired my boyhood imagination—tell a good story, but it is only the latest installment of a much longer tale. Most of life's history, at least 85% of it, is a history of microorganisms. The plants and animals so conspicuous in our own world are evolutionary later-comers, intercalated into ecosystems that were already 3 billion years old when sponges first gained a foothold on the seafloor. While the pattern of life's deep history has become clearer, however, we still don't understand fully the processes that drove the transitions between long-lasting states of the Earth system. Life certainly played a role, but so did tectonic changes on our dynamic planet. I suspect that the correct explanation will not point to physical or biological processes acting alone, but rather will emphasize the *interactions* between Earth and life. It has been, and continues to be, that interplay that guides evolution and environmental change through time.

Life, then, is not a feature of the Earth that stands apart from rocks, water, and air. Rather, life is an integral part of a highly interactive Earth system. Bacteria and archaea, with their dazzling diversity of metabolic processes, established ecosystems early in our planet's history, cycling carbon, sulfur, and nitrogen through primordial oceans. And more than 3 billion years later, despite millions of plant and animal species, microorganisms remain the fundamental cogs in the dynamic Earth system. Earth is a microbial planet—always has been, and always will be. We, on the other hand, are evolutionary upstarts, recent and quite possibly transient arrivals whose continuing well-being will depend in no small part on understanding how our actions influence the microbial world we inherited.

SUGGESTED READING

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